PROCEEDINGS

OF THE

BIOLOGICAL SOCIETY OF WASHINGTON

THE ORIGIN OF THE HAWAIIAN MONK SEAL

By Charles A. Repenning

U.S. Geological Survey, Menlo Park, California 94025

AND

Clayton E. Ray

Smithsonian Institution, Washington, D.C. 20560

The Hawaiian monk seal, *Monachus schauinslandi*, is a remotely located, seldom seen, and possibly vanishing species (Kenyon, 1972). Clearly, it was derived from some Atlantic population (Ray, 1976b). Two other species are assigned to the genus: the Caribbean monk seal, *M. tropicalis*, that may not have been seen since 1952 (Kenyon, 1973) and the Mediterranean monk seal, *M. monachus*, whose future survival must also be considered doubtful (Ronald, 1973).

In 1956 Judith E. King published a monograph on these three modern species of the genus *Monachus*. Her description included the comparative skeletal anatomy of the Caribbean and Mediterranean monk seals but omitted a discussion of the postcranial skeleton of the Hawaiian monk seal as no specimen was available to her. In 1961 King and Harrison described the skeletal and other anatomy of a juvenile of the Hawaiian monk seal, the first entire individual of this species to become available at the British Museum (Natural History) and possibly at any major museum in the world, although a juvenile skeleton has been in the collections of the U.S. National Museum of Natural History since 1913, and an adult skeleton since 1923. The skeleton, particularly the postcranial skeleton of the Hawaiian monk seal, has in any case remained poorly known and has received very little published attention.

On the basis of the examination by very few people of very few specimens, it has been widely assumed that the three

modern species of *Monachus* are similar animals. Most authors have regarded *M. schauinslandi* and *M. tropicalis* to be especially similar or closely related (King, 1956, p. 229; Davies, 1958, p. 488) if not conspecific (Scheffer, 1958, p. 37), although Rice (1973, p. 99) considered *M. schauinslandi* and *M. monachus* to be the more closely related. Repenning (1972) used the ear region of the Hawaiian monk seal, because of the availability of specimens, as an example of a primitive condition in living seals. He presumed without further inquiry, because of the scarcity of the other two species, that the ear region of all species of *Monachus* represented a similarly primitive condition. The assumption was repeated in another report (Hendey and Repenning, 1972) in which the first well-known fossil monachine seal was compared to other fossil and living seals, and the conclusion was made that *Prionodelphis capensis* from Pliocene rocks of South Africa had an ear region more specialized than that of the living species of *Monachus*. However, actual comparison was made only with *M. schauinslandi*, the Hawaiian species.

Nevertheless, in their study of the juvenile specimen of the Hawaiian monk seal that was received by the British Museum (Natural History) in 1958, King and Harrison (1961) noted several unusual anatomical features. Most of these were found in the pattern of specialization of the posterior vena cava which was very different from that of any seal so far described and appeared to represent a stage of development that might have occurred during the evolution of the pinniped posterior vena cava from the conventional fissiped abdominal vein. These authors suggested that the observed conditions might be primitive. They further suggested that these conditions might indicate that "the [Hawaiian] monk seals are not able to dive for so long a period or as deep as" most living genera of pinnipeds except the California sea lion, *Zalophus*. In their exception they extended their comparison to an anatomically different group of pinnipeds, the otarioids, but they did include in their comparison most genera of the phocoid pinnipeds, the group to which *Monachus* belongs. These suggestions were repeated by King (1964, p. 118). King and Harrison (1961) also noted in the innominate bone a foramen for the

obturator nerve posterior to the condyloid notch of the acetab-
ulum and anterior to the obturator fenestra. This foramen is
not present in other species of *Monachus* or in other phocoid
seals, although common in the otarioid pinnipeds. No conclu-
sion was drawn from the presence of this feature.

In 1966 King published a detailed comparison primarily of
the skeletal anatomy of the phocoid seals in order to explain
her simplification of their taxonomic subdivision into only two
subfamilies, the Phocinae and Monachinae. In this paper she
noted that several features of the genus *Monachus* appeared
to be less specialized than in other monachine seals, but she
made no mention of the degree of primitiveness of the three
living species of this genus relative to each other.

Thus, the first published statement since that of King and
Harrison (1961, repeated in King, 1964, p. 118, and also in-
ferred in Harrison and Kooyman, 1968, pp. 239–245) suggest-
ing that the Hawaiian monk seal might, in some respects, be a
uniquely primitive species of the genus *Monachus* was made
by Ray (1976b), who also made note of the isolated foramen
for the obturator nerve between the acetabulum and the ob-
turator fenestra of the innominate bone. Ray further noted
that in the Hawaiian monk seal the fibula was not fused proxi-
mally to the tibia, a distinctly fissiped character in carnivores
and not known in skeletally mature individuals of any other
pinniped except for primitive (fossil) otarioids and occasion-
ally in living walrus (Repenning and Tedford, in press). The
living walrus has been interpreted as retaining other features
considered to be primitive (Repenning, 1976). The immaturity
of the specimen examined by King and Harrison precluded any
possibility that they could have detected the lack of fusion
between the tibia and fibula in adulthood.

In 1976, while considering the biogeographic relations of
fossil and living pinnipeds (Repenning, Ray, and Grigorescu,
in press) we had occasion to note the osseous structures of the
ear of *M. tropicalis*, the Caribbean monk seal. To our surprise
they were much more specialized than those of the Hawaiian
monk seal, *M. schauinslandi*. It thus became imperative to
examine the osseous ear structures of the Mediterranean monk
seal, *M. monachus*, and one of the very few skulls available

was dissected. From this it was obvious that the very primitive otic structures ascribed to the genus *Monachus* by Repenning (1972) and Hendey and Repenning (1972) applied primarily to the Hawaiian monk seal. Although slightly less specialized as here defined, the ear region of the Caribbean monk seal most resembles that of the Pliocene fossil from South Africa, *Prionodelphis capensis*, now also known, at least generically, from the Atlantic coast of the United States (Ray, 1976b). Although slightly less specialized as here defined, the ear of the Mediterranean monk seal appears to be fairly similar to that of *Monotherium? wymani*, a Miocene fossil monachine about 14.5 million years old (Ray, 1976a). Thus, although all modern species of *Monachus* do seem to be characterized by a primitive degree of ear specialization, the specialization of the ear of the Hawaiian monk seal is more primitive than that of any known living or extinct species of monachine seal and probably of any phocoid seal, although the different configuration of the phocine petrosal makes this last comparison more difficult to judge.

The ear region may thus be grouped with the relations of the tibia and fibula, the posterior part of the vena cava, and possibly the nature of the innominate bone as features of the living Hawaiian monk seal that appear to be primitive. The retention of such primitive features implies a very long period of isolation of the Hawaiian monk seal from related forms in the North Atlantic and the southern hemisphere, an isolation more ancient than *Monotherium? wymani*. Some paleobiogeographic considerations mentioned by Repenning, Ray, and Grigorescu (in press) favor such an ancient isolation of this particular species.

Materials: In the National Museum of Natural History there is a large collection of skulls and one adult and two juvenile skeletons of *Monachus tropicalis*, many skulls and some 16 skeletons (mostly juveniles) of *M. schauinslandi*, and one adult and one juvenile skeleton of *M. monachus* with skulls. In addition, in the comparative collection of the U.S. Geological Survey in Menlo Park, California, there are 6 partial skulls of *M. schauinslandi* and an additional skull of *M. monachus*; these specimens will eventually be catalogued in the

National Museum of Natural History and the U.S. Geological
Survey numbers are temporary. For the purposes of this lim-
ited discussion, we have not attempted to review specimens in
other institutions, although our observations have been supple-
mented from the literature.

Specimens or casts of all fossil phocids pertinent to this
discussion have been available to us for examination, except
for a few highly significant but unstudied specimens from Peru
under the care of Robert Hoffstetter, Muséum National d'His-
toire Naturelle, Paris. These were mentioned briefly by Hoff-
stetter (1968). According to Hoffstetter's correspondence (to
Repenning, 1973) these phocid fossil remains of late Miocene
or early Pliocene age include a tibia and fibula that are un-
fused, although he made no mention of their maturity. If the
specimens are from mature individuals, they represent the
only known occurrence of this feature in phocoid seals except
for the living Hawaiian monk seal.

THE EAR

Although individually variable in detail and difficult to
evaluate functionally, the pinniped ear shows evidence of the
adaptation of a carnivore to the marine environment no less
conspicuous or remarkable than the evolution of flippers from
paws. The adaptation is basically a marine one, as shallow-
water aquatic carnivores have little or no modification of the
functional ear, but the adaptation is one for which selective
forces have strong and immediate influence once a carnivore
begins deep-water feeding.

Two factors are involved (Repenning, 1972): protection
against hydrostatic pressure, which has a relatively immediate
effect upon the ear structure of developing marine carnivores,
and directional sensitivity to hearing in water, which has a
selective force that is not so strong or immediate, at least as
indicated in the fossil record of otarioid pinnipeds (Repenning,
1976). The ability to withstand prolonged apnea, hence the
ability to make longer dives, also developed gradually in the
otarioid pinnipeds, and, hence, presumably in the phocoid seals
(Repenning, 1976).

From their observations of the structure of the posterior vena

cava of the Hawaiian monk seal, King and Harrison (1961), as noted above, suggested that this species may not be able to dive as deep or as long as other phocoid seals. They suggest that this may represent the persistence of an embryonic or primitive condition.

Similarly, the ear of the Hawaiian monk seal shows some indication of primitive deep diving adaptation. The osseous structure of the ear and the adjacent structures of the temporal bone appear to be well adapted to protection against hydro-static pressure. Nevertheless, the cavernous tissue lining the middle ear, which inflates with blood to prevent development of a relative vacuum as ambient pressure increases, is distrib-uted in the region of the epitympanic recess in a pattern quite unlike that of the other monachine and phocine seals (Repen-ning, 1972, pp. 315, 322). This pattern appears to parallel that of the otarioid pinnipeds, although at the present level of understanding such a parallelism seems as inexplicable as does the presence of a distinct obturator foramen widely separated from the obturator fenestra of the innominate bone, a feature common also in the otarioid pinnipeds. We are inclined to believe that both reflect some unknown primitive condition, as the separation of tibia and fibula reflects a known primitive condition.

In the case of the cavernous tissue in the middle ear of the Hawaiian monk seal, the unusual distribution of the tissue suggests considerable adaptive evolution independent from that shown in other phocoid seals. It should be noted, how-ever, that the distributional pattern of this tissue in the middle ear of the Caribbean and Mediterranean monk seals is un-known and is likely to remain so.

One phocoid feature that appears to be directly related to more sensitive hearing in water is quite weakly developed in the Hawaiian monk seal, less so than in any known fossil or living phocoid seal. This is the enlargement of the dorsal part of the petrosum (Pl. 1).

Along the medial side of the phocoid petrosum an upper and lower part may be defined by a line extending from the ves-tibular aqueduct forward across the top of the cochlear aque-duct to the anterodorsal surface of the apex. In many mona-

chines, including all species of *Monachus*, it is marked by a
groove that lies parallel to and slightly above the ventral petro-
sal sinus occupying the petrobasilar trench; in other mona-
chines, as *Leptonychotes*, the groove is obliterated by pachyo-
stosis of the petrosum.

As seen in Plate 1, the dorsal part of the petrosum in *M.
schauin landi*, as defined above, is smaller than the ventral
part which protrudes medially and apically from beneath the
dorsal part. In *M. tropicalis*, in dorsal view, the dorsal part
conceals the ventral part in all areas except those most postero-
medial and most apical; in addition the dorsal part is somewhat
more massive. In *Prionodelphis capensis*, the fossil seal from
South Africa (Hendey and Repenning, 1972), the postero-
medial area of the ventral part is mostly concealed (a small
spur of the dorsal part is broken off of the illustrated specimen
in this area) and the dorsal part of the petrosum is even more
robust, particularly at its apex. In the living *Leptonychotes
weddelli*, these modifications have reached their extreme.

Primary attachment of the petrosum to the mastoid part of
the temporal is via the ventral part of the petrosum, which
houses the cochlea, and thus progressive enlargement (espe-
cially apically) of the dorsal part, which houses the semicircu-
lar canals, increases the mass of the petrosum on the side of
the cochlea opposite to that of the primary attachment to the
mastoid. This progression is interpreted as reflecting increas-
ing sensitivity to waterborne sound, although it has no infer-
able relationship to sensitivity toward the direction of sound
(Repenning, 1972).

Enlargement of the dorsal part of the petrosum is at least
as great in *M. monachus* as in *M. tropicalis* and the degree of
development of this specialization is least, among all living
phocoid seals, in *M. schauinslandi*. In addition, the specializa-
tion of the dorsal part of the petrosum of *M. schauinslandi* is
less than that of any known fossil phocoid seal, including the
14.5-million-year-old *Monotherium? wymani* from Virginia
(Ray, 1976a).

In ventral aspect (Pl. 2) the lower part of the petrosum, as
here defined, is very similar in *M. schauinslandi* and *M. tro-
picalis* except that it is somewhat more robust in *M. tropicalis*
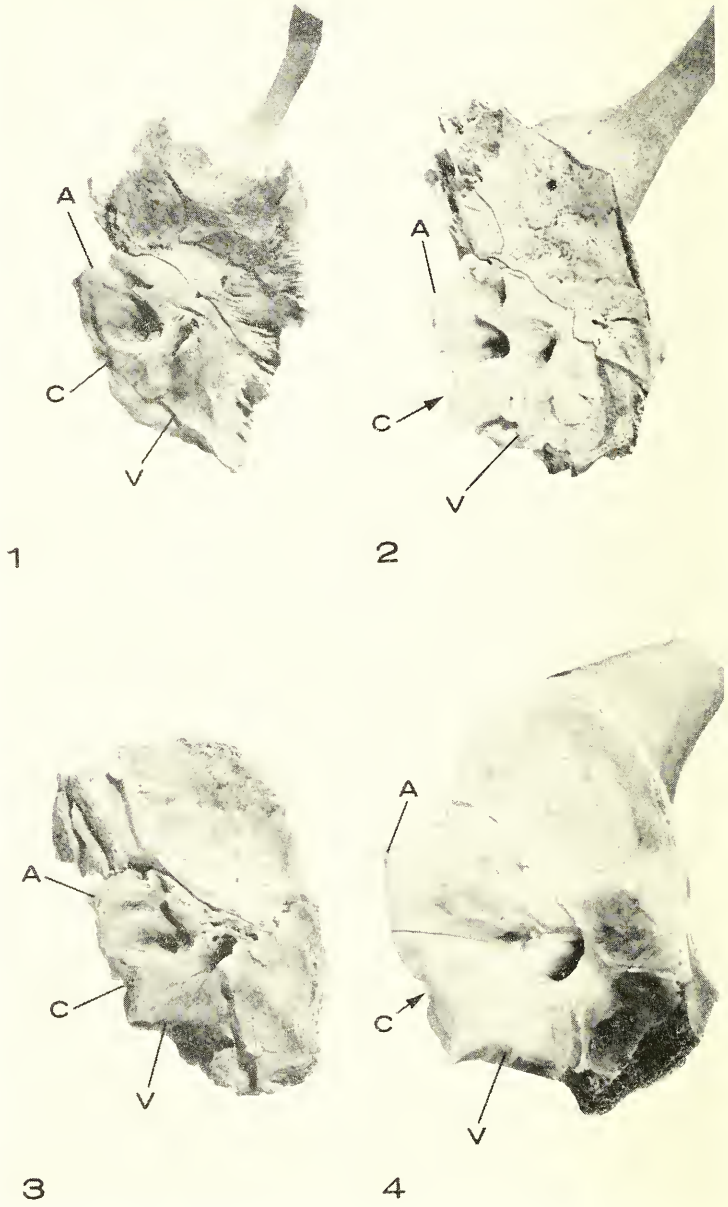
and the promontorium, largely formed by the basal whorl of the cochlea, is somewhat larger and has a slight secondary swelling anteromedial to the oval window and anterior to the round window in the Caribbean species. This slight second-ary swelling of the promontorium indicates a relative enlarge-ment of the apical whorls of the cochlea which is even more conspicuous on the petrosum of *M. monachus*. On the other hand, there is no tendency for such enlargement on the pro-montorium of *Leptonychotes weddelli* but, instead, it is char-acterized only by great exaggeration of the basal cochlear whorl.

Although enlargement of the entire cochlea may well indi-cate greater sensitivity in hearing, enlargement of the basal whorl only has been interpreted as reflecting increased sensi-tivity toward the direction of sound in water; it is the pattern followed by most phocoid seals (Repenning, 1972).

Thus, with respect to the structure of the cochlea, it appears that the living *Monachus schauinslandi* is the most primitive of known phocoid seals, although fewer fossils are available for comparison because the tympanic bullae are typically pre-served in place on the temporal bone of fossil seals. From the condition of the promontorium of *M. schauinslandi* increasing specialization could have followed a pattern of increasing sensitivity, as shown primarily by *M. monachus*, or a pattern of increasing sensitivity only in that part of the cochlea most significant to directional hearing, as shown in most living phocoids.

The ventral part of the petrosum of the fossil species, *Priono-delphis capensis*, appears, as does the dorsal part, to be inter-mediate between living *M. tropicalis* and *Leptonychotes wed-delli*. Not only is the medial lip of the dorsal part extended


←

PLATE 1.   Dorsomedial views of the right temporal bones of (1) *Monachus schauinslandi*, (2) *M. tropicalis*, (3) *Prionodelphis capensis*, and (4) *Leptonychotes weddelli* showing relative differences in size of the dorsal part of the petrosum. V = vestibular aqueduct, C = cochlear aqueduct, A = apex. Tympanic bullae have been removed except part remains on the fossil specimen of *P. capensis*. Anterior is up. Approxi-mately × ¾.
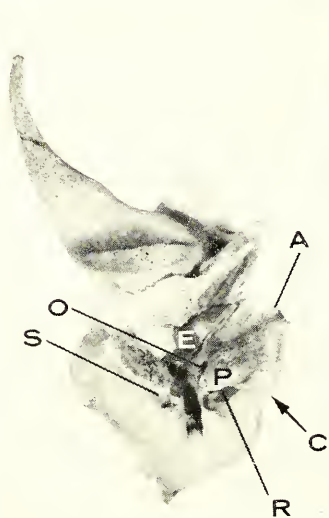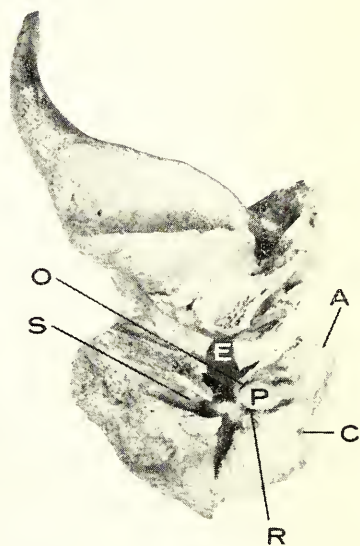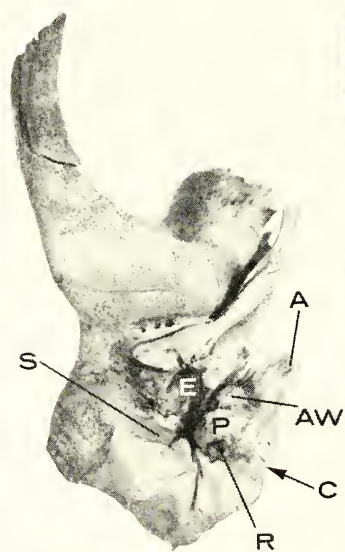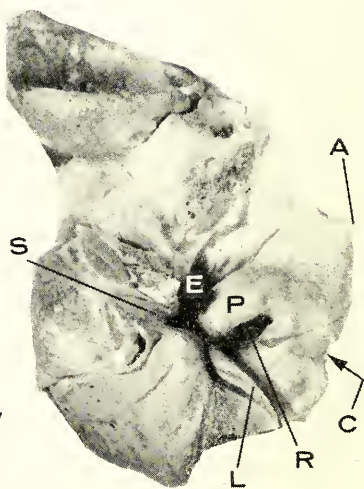
beyond the medial lip of the ventral part and the promontorium greatly swollen by enlargement only of the basal whorl of the cochlea, but also a conspicuous lip of the mastoid has developed which overlaps the posterior wall of the tympanic bulla (Pl. 3, figs. 1 and 2). Not unexpectedly, the ear region of this fossil species appears to be more specialized than do those of the living Caribbean and Hawaiian monk seals, and in all features reflecting such specialization *M. schauinslandi* from Hawaii appears to be extremely primitive. Moreover, the fossil *P. capensis*, on the basis of these similarities, seems to be only remotely related to the Mediterranean monk seal, as it appears to have different specializations in its ear relative to the part of the cochlea emphasized.

No conclusion is drawn from the auditory ossicles except that they show considerable interspecific differences. Upon gross examination, the head of the incus of *M. tropicalis* appears to be relatively the least developed and the incudomalleolar articulations form a single confluent saddle-shaped articulation as described by King (1969, p. 12), and confirmed on additional specimens by Ray (1976a, p. 18), for *Ommatophoca*; the first would suggest minimal specialization and the latter great specialization.

Postcranial Skeletal Peculiarities

King and Harrison (1961, fig. 4a) and Ray (1976b, fig. 4) have noted and illustrated the presence of a separate foramen for the obturator nerve midway between the acetabulum and

---

←

Plate 2.   Slightly lateral of ventral views of the temporal bones of (1) *Monachus schauinslandi*, (2) *M. tropicalis*, (3) *M. monachus*, and (4) *Leptonychotes weddelli* showing differences in form of the promontorium of the petrosum related to variations in specialization of the cochlea. A = apex, C = cochlear aqueduct, P = promontorium, O = oval window [hidden in (3) and (4)], R = round window, E = epitympanic recess, S = stylomastoid foramen, L = lip of the mastoid on *Leptonychotes* that overlaps the posterior part of the bulla, and AW = secondary swelling of the promontorium of *M. monachus* that houses apical whorls of the cochlea. Tympanic bullae have been removed and anterior is up. Approximately × ¾.

1
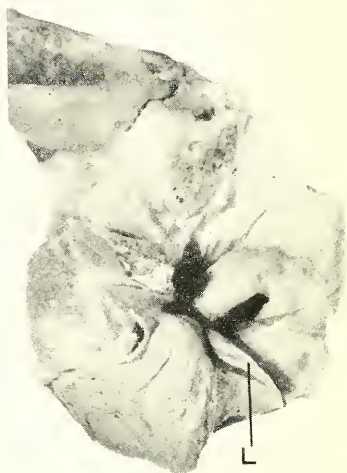
2

3

4

the obturator fenestra in the innominate bone of the Hawaiian monk seal. This foramen is present on both sides in all individuals of *M. schauinslandi* in the National Museum of Natural History. It is of large caliber, 5 mm or more in many instances; fully developed even in newborn individuals; confined to the pubis, or in at least one case bordering the anterior pubo-ischiadic suture; and penetrates the thick body of the bone, generally closer to the acetabulum than to the obturator fenestra. Although a similar foramen is variably present in living otarioid pinnipeds, most commonly in the fur seals, *Arctocephalus* and *Callorhinus*, we are aware of its occurrence in no other living or fossil phocoid, including the early phocine forms, *Leptophoca lenis*, for which several innominate bones are available, and *Phoca vindobonensis*. Unfortunately, the innominate bone is unknown for *Monotherium? wymani*, the oldest monachine.

Some individuals of some species of modern phocoids have a more or less strongly marked notch or channel at the anterior extremity of the obturator fenestra, probably homologous to the obturator foramen of *M. schauinslandi*. This channel seems to be especially well marked in some individuals of *Cystophora*, for example. We have noted closure of the notch unilaterally by a narrow, thin bridge of bone in one specimen of *Hydrurga* and in two of *Phoca vitulina* among the many phocoid skeletons available to us, including at least one of every living species. These foramina however are scarcely comparable to those in *M. schauinslandi* in that they are uncommon, unilateral, and marginal to the obturator fenestra, from which they are only weakly separated apparently late in life. Interestingly, of innominate bones of two adult individ-

---

←

PLATE 3. Ventral views of the temporal bones of (1) *Prionodelphis capensis* and (2) *Leptonychotes weddelli*. L = lip of mastoid that overlaps posterior wall of bulla. Anterior is up. Dorsal views of the temporal bones of (3) *Monachus schauinslandi* and (4) the 14.5-m.y.-old *Monotherium? wymani* to show relative enlargement of the dorsal part of the petrosum. The photograph of the temporal bone of *Monotherium? wymani* is taken from Ray (1976a) and is shown at natural size; all other photographs are approximately × ¾.

uals of *M. tropicalis* illustrated by Allen (1887, Pl. 4, figs. 4 and 5), one shows a well marked notch and the other a fully closed foramen. In the one old adult skeleton of *M. tropicalis* available to us, a foramen is almost completed in the left innominate bone only, by thin projections of bone separated by a very narrow gap. The foramen, as strongly developed and uniformly present in *M. schauinslandi* at least from birth, seems to us to be a primitive feature unique to that species among known fossil and modern phocoid seals.

Ray (1976b, fig. 5) has also noted that all available skeletons of the Hawaiian monk seal have the proximal epiphysial head of the fibula unfused to the epiphysial head of the tibia; in individuals mature enough to evaluate (at least 6 in the National Museum collections), distinct articular facets are present at contiguous points of these two bones. Except occasionally on one or both sides in living walrus (interpreted by Repenning, 1976, as retaining other primitive features), this condition also is unknown in living pinnipeds and is unknown, with one possible exception, in all fossil phocoid seals including *Monotherium?* *wymani* (Ray, 1976a) and *Leptophoca lenis*. However, Repenning and Tedford (in press) report this condition in early otariid otarioid pinnipeds, forms probably between 7 and 8 million years old. Work we have in progress indicates that pinnipeds ancestral to the otariids were characterized by separate tibia and fibula, which is understandable as they were derived from fissiped carnivores (Mitchell and Tedford, 1972).

Although she stated that the two bones are fused proximally as usual in pinnipeds, King (1956, pp. 241, 250) did note that in only one of two adult skeletons of *M. monachus* was the fibula fused to the tibia, and in that instance only on one side. She suggested that this fusion must be among the last to occur. In the one adult *M. monachus* available to us the tibia and fibula are fused proximally on both sides. We are somewhat uncertain as to whether or in which instances King's statements apply to coossification between the proximal epiphyses of the tibia and fibula or to fusion of each epiphysis with its diaphysis, but in any event, we regard the coossification between tibia and fibula as typical of adult *M. monachus*, pending examination of more specimens. In species in which proximal coossifi-

cation occurs with age, the condition may be anticipated in younger animals by the sutural contact between the two elements, rather than by a faceted contact as in *M. schauinslandi*. Further, in these species the proximal epiphyses typically coossify with one another before either fuses with its respective diaphysis.

The one apparent example mentioned above in the fossil record of phocoids in which the tibia and fibula remain separate is an undescribed record from Sacaco, Peru, briefly mentioned by Hoffstetter (1968). In correspondence (to Repenning, 1973) Hoffstetter has stated that the phocoid seal from Sacaco has an unfused tibia and fibula and is broadly estimated as being late Miocene or early Pliocene in age, or about 5 million years old. The maturity of the individual was not mentioned. Although undescribed and certainly vague in details, this could well be a highly significant record.

Should the Peruvian fossil be from an adult, it would suggest that this seal belonged to a population which, like the ancestor of the Hawaiian monk seal, became separated from the Atlantic-Caribbean monachines at a very early date (perhaps 15 million years ago) and could, therefore, indicate a much more ancient separation of the antarctic monachines from the ancestral monachines of the North Atlantic than presently supposed. The fossil phocoids from Peru are associated with fossil otarioids (Hoffstetter, personal commun., 1973) and are the oldest (some 5 million years) recorded pinnipeds in the southern hemisphere. However, the remarkably abundant remains of *Prionodelphis capensis* from South Africa may be little more than a million years younger and no otarioid remains are known in this area; the oldest fossil otarioid known from South Africa (Hendey, 1974) is much less than one million years old. Possibly, as suggested by Repenning, Ray, and Grigorescu (in press), the Peruvian fossils do not represent the oldest phocoid in the southern hemisphere.

POSTERIOR VENA CAVA

Elsner (1969, pp. 138–140) has summarized the differences between the posterior venae cavae of the pinnipeds and those of terrestrial mammals, and he has outlined his experimentation

showing that these pinniped modifications of the basic mammalian pattern enable the storage of a great quantity of well-oxygenated blood which, in turn, enables the seal to prolong greatly its time of apnea during dives. Harrison and Kooyman (1968, pp. 239–247) summarize in more detail the anatomy of the pinniped venous system and outline the differences between the abdominal veins of otarioid and phocoid pinnipeds. In this discussion they frequently refer to the work of King and Harrison (1961) on the Hawaiian monk seal, pointing out how it differs from the general phocoid pattern.

In fissiped carnivores the posterior vena cava is of conventional mammalian pattern beginning with the union of the common iliac veins and running anteriorly as a single trunk to the diaphragm. The principal tributaries are the left and right renal veins, the left being somewhat more elongate and complicated because of secondary tributaries, and, more anteriorly, the hepatic veins. In most phocoid seals the posterior vena cava is bifurcate in and posterior to the region of the renal tributaries, which are multiple to accomodate the circulatory specialization of the kidneys. Anterior to the renal tributaries the right and left branches of the postcava unite to form a single large trunk running forward to the region of the hepatic veins where it is greatly inflated into a hepatic sinus. The hepatic sinus and the large and distensible posterior vena cava, including left and right branches, can store a great volume of blood relative to the size of the animal. Elsner and others (1964) indicate that the posterior vena cava of the northern elephant seal is capable of holding about one fifth of the total body blood.

In addition to the spectacular storage capacity of the phocoid posterior vena cava, it contains, at the diaphragm, a sphincter that regulates the flow of stored blood to the heart during diving (Hol, Blix, and Myhre, 1975).

In all of these phocoid specializations, the exception is the Hawaiian monk seal. King and Harrison (1961) described the posterior vena cava as being duplicated, but, in the region of the renal tributaries there is a complex network of anastomotic channels, and some renal tributaries join the postcava anterior to the principal bifurcation. The hepatic sinus is only slightly

inflated and still retains falciform septa, relics of the walls of those parts of the hepatic veins that have become incorporated in the sinus, and the sphincter at the diaphragm is incomplete.

From their illustration (King and Harrison, 1961, p. 290) it would appear that the right branch of the postcava is the original trunk of the fissiped posterior vena cava and that the left branch probably developed from the left renal vein of the fissipeds. A similar interpretation was made of the posterior vena cava of *M. monachus* in 1927 by Dieuzeide; however, he described no complex network of anastomoses. The network of anastomotic channels noted by King and Harrison certainly looks like drainages from the stellate renal plexus of the left kidney that are relics of a still more primitive marine phocoid that retained a fissiped-like, unbranching posterior vena cava with an unenlarged left renal vein.

There is, of course, no fossil record of the development of the distinctly phocid pattern of the posterior vena cava. However, as with other specializations described above, the relatively undeveloped specializations of the posterior vena cava of the Hawaiian monk seal that set it apart from other phocoid seals resemble the condition found in the otarioid pinnipeds, as pointed out by King and Harrison (1961) and Harrison and Kooyman (1968).

Whether these features of the Hawaiian monk seal that we have discussed represent parallel specializations or retained primitive features may not be clear in all cases, but certainly they all suggest that *M. schauinslandi* may well be regarded as the most primitive of living seals.

BIOGEOGRAPHIC CONSIDERATIONS AND CONCLUSIONS

Repenning, Ray, and Grigorescu (in press) discuss at some length the biogeographic significance of the available distributional and evolutionary history of the pinnipeds including that of *Monachus schauinslandi* in the Hawaiian Islands. They conclude that this seal was derived from the North Atlantic, probably from a Caribbean population, both because of the nature of the North Atlantic fossil record and because of the

existence of a Central American seaway separating North and South America.

The available evidence suggests that the Hawaiian monk seal may have been separated from its ancestral population more than 15 million years ago. The unspecialized features of the Hawaiian monk seal discussed above are more primitive than those of the oldest known fossil monachine seal, approximately 14.5 million years old. This date correlates with the maximum in oceanic temperatures 15 million years ago, thus favoring a Caribbean seal crossing half the Pacific Ocean, and also approximates the most recent time that the full force of the Atlantic equatorial currents passed between North and South America and joined the Pacific North Equatorial Current, thus assisting the westward dispersal with both current and temperature. Finally, the known tectonic-volcanic history of the Hawaiian Island chain indicates that there were at least some islands present to colonize.

The Hawaiian monk seal, therefore, appears to be the modern representative of the most ancient of living phocoid lineages, and as such might be characterized not altogether improperly as a "living fossil". Of all living pinnipeds only the walrus approaches such a genealogical distinction, but available fossil evidence seems to indicate that its lineage, which includes many extinct forms, probably began somewhat more recently (Repenning and Tedford, in press). The several uniquely primitive anatomical features of the Hawaiian monk seal and its very poorly known anatomy and virtually unknown behavioral and adaptive characteristics suggest that much insight into pinniped natural history might be gained from its study. The opportunity for such a study of its closest relatives has almost certainly been lost irrevocably in the case of *M. tropicalis* from the Caribbean and probably most of the social characters of *M. monachus* have already been drastically altered through human intervention. Without immediate attention the anatomy and physiology of the Mediterranean monk seal will also remain forever virtually unknown.

The survival of the Hawaiian monk seal is not at all ensured. It is a unique mammal, thorough understanding of which might well improve our understanding of all seals. Obviously

a better understanding of *Monachus schauinslandi* would enhance its chances for survival. If it is justifiable to make distinctions in the relative importance of species, then *M. schauinslandi* has to be assigned high priority. Therefore we are encouraged to recommend that comprehensive, careful, and sustained studies of the Hawaiian monk seal be carried out very soon.

Acknowledgments

Literature Cited

Allen, J. A.   1887.   The West Indian seal (*Monachus tropicalis* Gray). Bull. Amer. Mus. Nat. Hist. 2(1):1–34.

Davies, J. L.   1958.   The Pinnipedia: an essay in Zoogeography. Geogr. Rev. 48(4):474–493.

Dieuzeide, R.   1927.   Sur quelques points d'anatomie du phoque-moine de la Méditerranée (*Monachus albiventer* Boddaert). Bull. Stat. Aquiculture Pêche Castiglione 1927 (2):213–249.

Elsner, R.   1969.   Cardiovascular adjustments to diving. Ch. 5:117–145. *In* H. T. Andersen (ed.). The biology of marine mammals. Academic Press, New York and London.

ELSNER, R., P. F. SCHOLANDER, A. B. CRAIG, E. G. DIMOND, L. IRVING, M. PILSON, K. JOHANSEN, AND E. BRADSTREET. 1964. A venous blood oxygen reservoir in the diving elephant seal. Physiologist 7:124.

HARRISON, R. J., AND G. L. KOOYMAN. 1968. General physiology of the Pinnipedia. Ch. 7:211–296. *In* R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman (eds.). The behavior and physiology of pinnipeds. Appleton-Century-Crofts, New York.

HENDEY, Q. B. 1974. The late Cenozoic Carnivora of the southwestern Cape Province. Ann. South African Mus. 63:1–369.

HENDEY, Q. B., AND C. A. REPENNING. 1972. A Pliocene phocid from South Africa. Ann. South African Mus. 59(4):71–98.

HOFFSTETTER, R. 1968. Un gisement de vertébrés tertiaires a Sacaco (Sud–Pérou), témoin Néogène d'une migration de faunes australes au long de la côte occidentale Sud-Américaine. Acad. Sci. Paris, C. R., Ser. D, 267:1273–1276.

HOL, R., A. S. BLIX, AND H. O. MYHRE. 1975. Selective redistribution of the blood volume in the diving seal (*Pagophilus groenlandicus*). pp. 423–432. *In* K. Ronald and A. W. Mansfield (eds.). Biology of the seal. Rapp. Réun. Cons. Int. Explor. Mer, 169.

KENYON, K. W. 1972. Man versus the monk seal. Jour. Mammal. 53(4):687–696.

———. 1973. Hawaiian monk seal (*Monachus schauinslandi*). pp. 88–97. *In* Seals. Int. Union Cons. Nature publs., n.s., Suppl. Pap. 39.

KING, J. E. 1956. The monk seals (genus *Monachus*). Bull. British Mus. (Nat. Hist.), Zool. 3(5):201–256.

———. 1964. Seals of the World. British Mus. (Nat. Hist.), London. 154 pp.

———. 1966. Relationships of the Hooded and Elephant seals (genera *Cystophora* and *Mirounga*). Jour. Zool. 148:385–398.

———. 1969. Some aspects of the anatomy of the Ross seal, *Ommatophoca rossi* (Pinnipedia:Phocidae). British Antarc. Survey, London. Sci. Repts. 63:54 pp.

KING, J. E., AND R. J. HARRISON. 1961. Some notes on the Hawaiian monk seal. Pacific Sci. 15(2):282–293.

MITCHELL, E. D., AND R. H. TEDFORD. 1972. The Enaliarctinae: a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. Bull. Amer. Mus. Nat. Hist. 151(3):201–284.

RAY, C. E. 1976a. *Phoca wymani* and other Tertiary seals (Mammalia: Phocidae) described from the eastern seaboard of North America. Smithsonian Contrib. Paleobiol. No. 28:36 pp.

———. 1976b. Geography of phocid evolution. Syst. Zool. 25(4):391–406.

REPENNING, C. A. 1972. Underwater hearing in seals: functional mor-

phology. pp. 307–331. *In* R. J. Harrison (ed.). Functional anatomy of marine mammals, Vol. 1. Academic Press, London and New York.

————. 1976. Adaptive evolution of sea lions and walruses. Syst. Zool. 25(4):375–390.

REPENNING, C. A., C. E. RAY, AND D. GRIGORESCU. In press. Pinniped Biogeography. *In* A. J. Boucot and J. Gray (eds.). Historical biogeography, plate tectonics, and the changing environment. 37th Biological Colloquium of the Oregon State University, Corvallis. Univ. Oregon Press.

REPENNING, C. A., AND R. H. TEDFORD. In press. Otarioid seals of the Neogene. U.S. Geol. Survey Prof. Paper 992.

RICE, D. W. 1973. Caribbean monk seal (*Monachus tropicalis*). pp. 98–112. *In* Seals. Int. Union Cons. Nature publs., n.s., Suppl. Pap. 39.

RONALD, K. 1973. The Mediterranean monk seal, *Monachus monachus*. pp. 30–41. *In* Int. Union Cons. Nature publs., n.s., Suppl. Pap. 39.

SCHEFFER, V. B. 1958. Seals, sea lions, and walruses. Stanford Univ. Press, Stanford, California, x + 179 pp.